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Branched prothallia in the Polypodiaceae*

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(WITH FIFTEEN TEXT FIGURES)

Introduction

Branching in the early stages of the gametophytes of the Polypodiaceae has received little attention in the literature. Branching in older prothallia by means of adventitious outgrowths arising from any part of the prothallium has been described for various genera by Wiegand ('49), Hofmeister ('51), Kny ('70), Goebel ('77), De Bary ('78), Bauke ('78), Dodel-Port ('80), Klebs ('93), Heim ('96), Lagerburg ('06), Pace ('10), Heilbronn ('10), Fischer ('11), Schlumberger ('11), Wuist ('13), Pickett ('14), and Black ('15). Few cases have been cited where branching took place at an early period in the development of the gametophyte, except in the case of *Vittaria* which has been described and figured by Britton and Taylor ('02). As it is characteristic of the prothallia of that genus to branch extensively, resembling in this respect the gametophytes of the Hymenophyllaceae, no examples will be cited. Among the other genera of the Polypodiaceae the following cases of branching, while the prothallia were still in the filamentous stage, have been noted. Beck ('80) described branched prothallia of *Scolopendrium vulgare* Sm., while Klebs ('93) by means of weak light obtained, in *Polypodium aureum* L., branched prothallia with adventitious outgrowths. Atkinson ('94) observed "in *Adiantum cuneatum* . . . some curious forms of starved prothallia," and added: " In one case, first noted by a student, the protonemal thread forked a short distance from the spore, and the branches extended at right angles to the primary thread like the arms of the letter T, each arm bearing a prothallium. In another case observed the young prothallium produced nearly colourless protonemal threads from marginal cells. Each of these threads bore a prothallium, and in turn produced marginal threads bearing other prothallia." Lagerburg ('06) figured a slightly branched filamentous male gametophyte of *Pteridium aquilinum* (L.) Kuhn. Pace ('10) described branched filamentous prothallia of an unknown genus, and Black ('15) observed extensive branching among the filamentous prothallia of *Onoclea sensibilis* L. which had grown in a submerged condition in cultures of distilled water.

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* Contribution from the Osborn Botanical Laboratory.

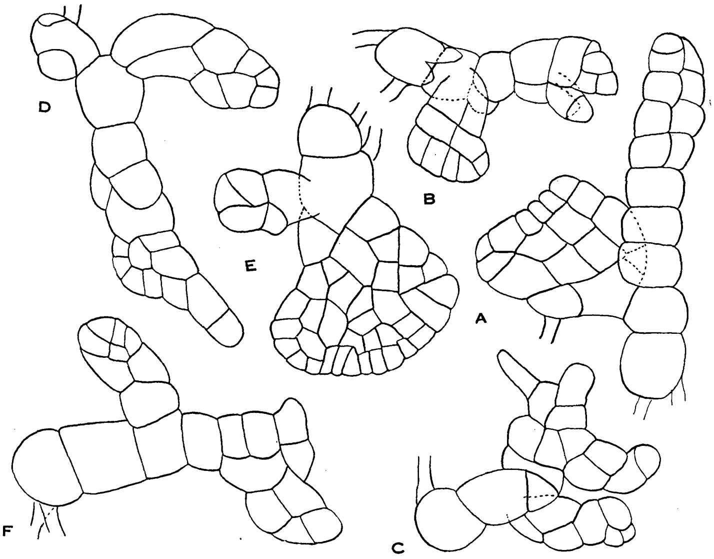

FIG. 1. Branched prothallia of *Onoclea sensibilis* L., × 125.

MATERIAL

The branched prothallia described in this paper occurred in cultures which had been made for the study of the comparative length of the filamentous stage in various genera of the Polypodiaceae. The genera which showed a tendency to branch were the following: *Adiantum*, *Asplenium*, *Camptosorus*, *Onoclea*, *Phegopteris*, *Polypodium*, *Pteridium*, *Scolopendrium*, *Woodsia* and *Woodwardia*. The spores of these various genera were obtained from several sources. Those of *Adiantum* were secured from the greenhouse of the botanical department, Cornell University, and those of *Phegopteris* came from a lawn in Ithaca, New York. The spores of *Camptosorus* and *Scolopendrium* were collected in eastern New York by Mr. Ten Eyck Burr; while those of *Asplenium*, *Onoclea*, *Pteridium* and *Woodsia* were obtained from the wild botanical gardens of Minneapolis, Minnesota, through the courtesy of Miss Eloise Butler. The spores of *Woodwardia* were collected near Ann Arbor, Michigan.

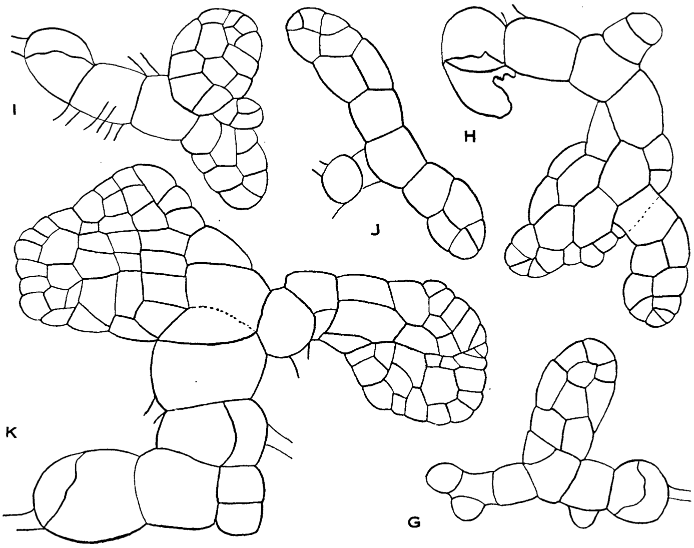

FIG. 2. Branched prothallia of *Onoclea sensibilis* L., × 125.

Cultures of these genera were made by sowing the spores on distilled water and on soil. A series of cultures of *Camptosorus*, *Phegopteris*, *Pteridium*, *Onoclea*, *Scolopendrium*, and *Woodwardia* were made by sowing the spores on Knop's and Prantl's full solutions and on certain modifications of these solutions.

The formulas used in making up Knop's and Prantl's ('81) nutrient solutions are as follows:

Knop's Solution	
$MgSO_4$	0.25 g.
$Ca(NO_3)_2$	1.00 g.
K_2HPO_4	0.25 g.
KCl	0.12 g.
$FeCl_3$	trace

Prantl's Solution	
K_2SO_4	0.7 g.
$NaCl$	0.23 g.
$CaSO_4$	0.7 g.
$MgSO_4$	0.5 g.
Na_3PO_4	0.5 g.
NH_4NO_3 solution, 0.064 per cent.	20 c.c.

The modifications employed were the following:

Knop's Solution
(*a*) $Ca(NO_3)_2$ omitted

Prantl's Solution
(*a*) NH_4NO_3 omitted
(*b*) NaCl and Na_3PO_4 omitted
(*c*) NaCl omitted
(*d*) Na_3PO_4 omitted
(*e*) $CaSO_4$ omitted

After the spores were sown, the cultures were placed before an east window where the conditions of light and temperature were approximately the same for all.

Description of the branched prothallia

In all the cases observed, the germination of the spores, the manner and the rate of growth in the branching prothallia did not differ from that of the unbranched prothallia. Neither were the branched prothallia limited to one kind of culture, but were found in all three kinds. In some of the genera they appeared simultaneosluiyn the three kinds of cultures.

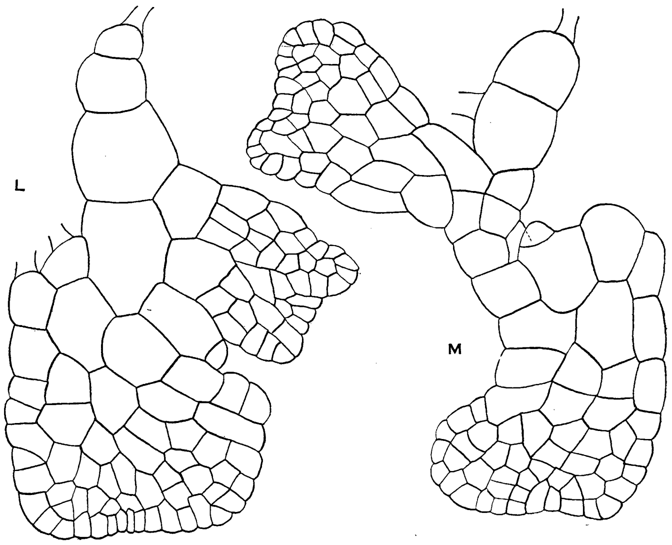

Fig. 3. Branched prothallia of *Onoclea sensibilis* L., × 75.

Onoclea sensibilis L.—The prothallia of this species both on the distilled water and the soil cultures showed a decided tendency to branch. Likewise, the branches showed a great diversity of origin and form, and the beginnings of apical cells or more advanced apical growth was present in all of them. The branched prothallia shown in FIGS. 1, A–F; 2, G–J; 4, N–Q; and 5, R–T, developed on the distilled water cultures, while those in FIGS. 2, K; 3, L, M; and 5, U, developed close to the inner pot wall on the soil cultures. FIG. 1, A, D, shows branched prothallia whose branches originated in the second cell of the filament. In these prothallia the branches tended to form immediately a plate of cells, while the cells of the filaments continued to divide transversely until three and five cells were formed before they developed an expanded region. In FIG. 1, B, C, while the first branches developed from the second cell of the filament, later branches were given off by the expanded portions of the prothallia. FIG. 1, D, shows not only the development of a branch from the second cell of the filament but also the tendency of the prothallium to revert to a filamentous stage after a small plate of cells has been formed, if the nutrition is not sufficient to meet its needs. In FIGS. 1, F; and 2, G, H, it seems characteristic for the first branch to originate in the third cell of the filament. However, other branches developed from the more expanded portion of the prothallia. FIG. 2, I, J, shows pronounced cases of dichotomous branching which occurred where

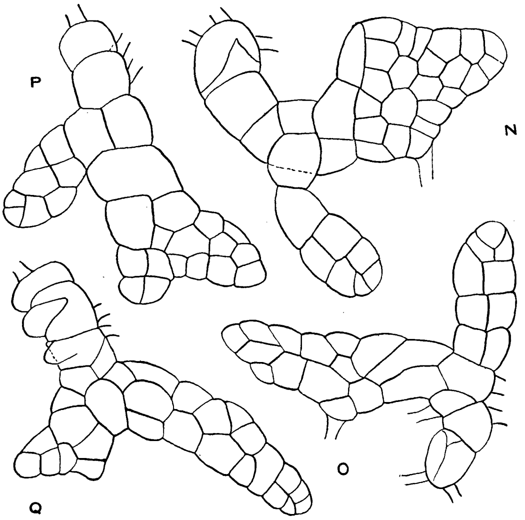

FIG. 4. Branched prothallia of *Onoclea sensibilis* L., × 125.

the filament usually gave rise to the expanded portion of the prothallium. In both of these cases the branches originated in the third cell of the filament. In FIG. 2, J, the group of cells at the apex between the branches indicate that there will be a continuation of the main growth of the prothallium. In FIGS. 2, K, and 3, L, M, dichotomous branching developed at a slightly later stage after the first divisions of the expanded portion of the prothallia had been formed. FIG. 4, N–Q, show single lateral branches which appear to have originated at about the same period in the development of the prothallia as the dichotomous branches shown in FIGS. 2, K, and 3, L, M. FIG. 5, R, S, shows branches developed from the expanded portions of the prothallia. In FIG. 5, R, the branch formed a plate of cells while in FIG. 5, S, it tended to assume a filamentous character. FIG. 5, T, shows another case of dichotomous branching but at a later stage in the development of the prothallium. Here it occurred at the apex of the expanded region of the young prothallium. FIG. 5, U, is unique in that the branch appears to have originated in the first, second and third cells of the filament.

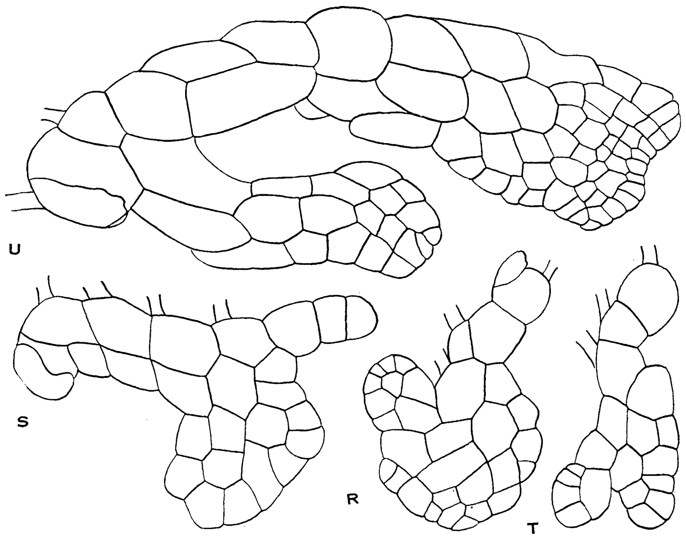

FIG. 5. Branched prothallia of *Onoclea sensibilis* L. R–T, × 125; U, × 75.

Adiantum bellum Moore.—Branched prothallia in the various species of *Adiantum* studied occurred only on the distilled water cultures. In FIG. 6, A, is shown the only case of branching which was observed *in A. bellum.* Here the filamentous branch originated in the first cell of the filament.

Adiantum Capillus-Veneris L.—Examples of branching among the prothallia of this species were frequently observed. In all cases the branching was monopodial and in the majority of cases, as shown in FIG. 6, B–G, the branches developed from the second cell of the filament. FIG. 6, C–E, shows the manner of development of the branch and likewise the continued growth of the main filament. In FIG. 6, F, no filament had been developed; the second cell divided to form the beginnings of the expanded portion of the prothallium. From this expanded region the branch was given off.

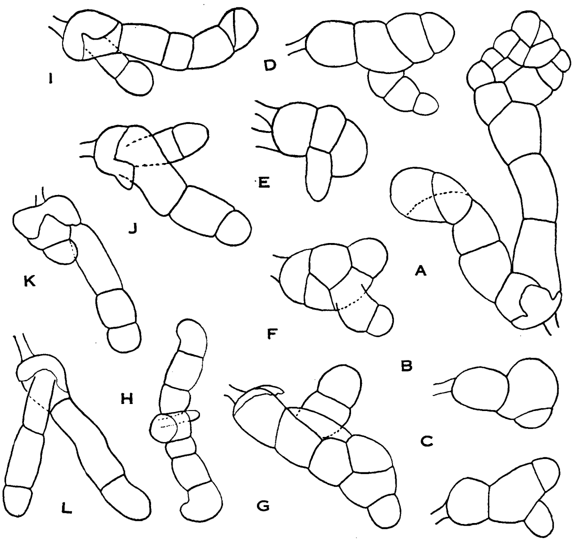

FIG. 6. A. Branched prothallium of *Adiantum bellum* Moore, × 175. B–G. Branched prothallia of *A. Capillus-Veneris* L., × 125. H. Branched prothallium of *A. cardiochloena* Kunze, × 125. I–L. Branched prothallia of *A. cuneatum* Langsd. & Fisch., × 125.

Adiantum cardiochloena Kunze.—FIG. 6, H. Here the branch developed from the cell which was cut off by the formation of a vertical wall in the second cell of the filament.

Adiantum cuneatum Langsd. & Fisch.—FIG. 6, I–L. Branching in this species occurred at an early stage in the development of the prothallia. The branches originated in the first cell of the filament and the growth in all cases was very rapid. In FIG. 6, L, is shown a prothallium with a branch as long as the main filament.

Adiantum trapeziforme L.—FIG. 7, A–G, represents branched prothallia of this species. Here branching was both dichotomous and monopodial. In FIG. 7, E, is shown an unusual case of dichotomous branching where both branches tended to grow in the same direction.

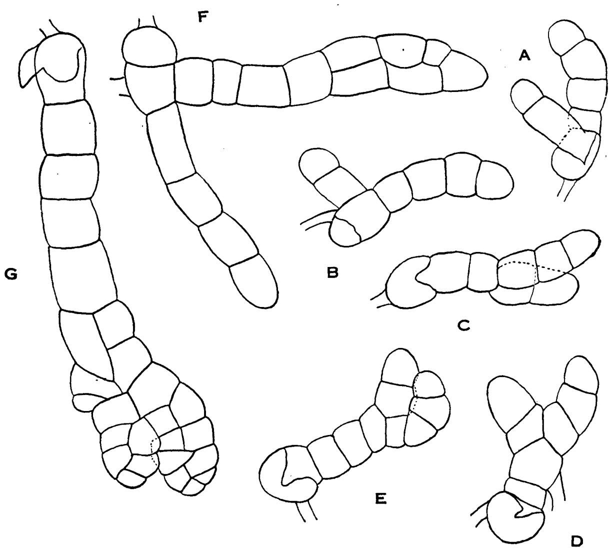

FIG. 7. Branched prothallia of *A. trapeziforme* L., × 125.

Camptosorus rhizophyllus (L.) Link.—FIG. 8, A–D, shows branched prothallia of this species which developed on the distilled water cultures, while FIG. 8, E, shows a prothallium which developed on the inner surface of the pot wall of the soil cultures. FIG. 8, A–D, shows the beginnings of branching in very young prothallia. Branching in two of the cases was dichotomous and in the other two cases monopodial. A few days after the spores were sown on the distilled water, germination took place in the normal manner. In FIG. 8, A, the first prothallial cell instead of dividing by a transverse wall to form a filament of two cells, cut off by two oblique longitudinal walls, a branch cell on either side. FIG. 8, B, C, shows similar cases, however in FIG. 8, B, the second instead of the first prothallial gave rise to the branches. In FIG. 8, C, both the second and third cell each gave rise to a branch while the third cell of the filament continued the growth of the prothallium. In FIG. 8, D, the branch cell which developed from the first prothallial cell divided immediately to form the beginning of a plate of cells. The branched prothallium shown in FIG. 8, E, is in a much more advanced stage of development. Here a filament of four cells was formed, then a plate of cells developed. From this plate, early in its development, a lateral branch was cut off which in turn formed an expanded prothallium. The original plate of cells continued its growth into a broad prothallium which showed a decided tendency to branch at its apex.

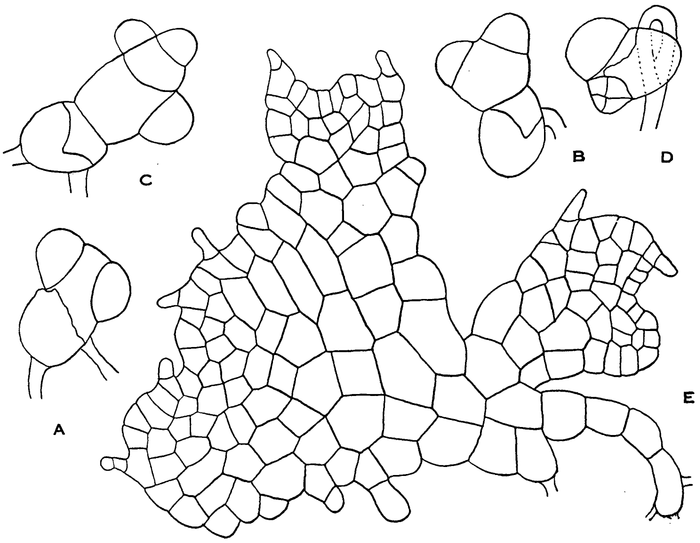

FIG. 8. Branched prothallia of *Camptosorus rhizophyllus* L. A–D, × 125; E, × 75.

Asplenium Filix-femina (L.) Bernh.—The branched prothallia of *A. Filix-femina* were observed on both the soil and distilled water cultures. FIG. 9, A, B, developed on the distilled water cultures and FIG. 9, C, on the inner surface of the pot wall where the light conditions were good and the prothallium was not crowded by other prothallia. FIG. 9, A, shows a young branched prothallium of about twenty cells, which had formed a filament of three cells in the usual manner before the expanded portion of the prothallium developed. The second cell of this filament gave rise to a filamentous branch of three cells; the terminal one of which divided by two oblique longitudinal walls to form the beginnings of an apical cell. From the first cell of the branch was cut off laterally a cell which would later develop into another branch. The expanded portion of the prothallium also gave rise to a short filamentous branch of two cells.

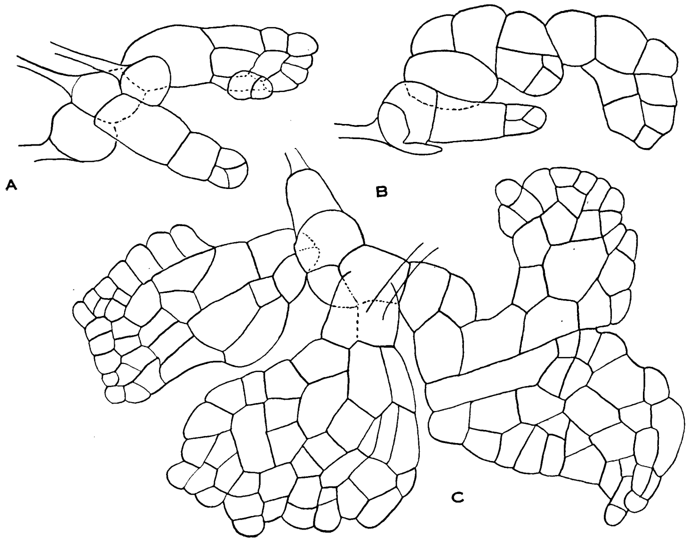

FIG. 9. Branched prothallia of *Asplenium Filix-femina* (L.) Bernh., × 75.

In FIG. 9, B, a short filament of three cells was first formed by transverse divisions, then the third cell divided in such a manner as to form the beginnings of an apical cell. In the meantime a cell was cut off laterally from the first cell of the filament. By transverse and longitudinal divisions this branch developed becoming two cells in width and forming at the apex the beginnings of an apical cell. An extreme case of branching is shown in FIG. 9, C. A filament of three cells formed in the usual manner. From the second cell there was cut off laterally a cell which developed immediately by longitudinal and transverse divisions into an expanded branch with a definite growing region at the apex. The third cell of the original filament divided by a longitudinal division into two cells, a larger and a smaller one. From the larger of these two cells a branch developed which formed another expanded prothallium whose growing point was not definitely marked. In the meantime the growth of the primary prothallium had continued and an expanded part was formed showing a decided tendency to branch dichotomously at the apex.

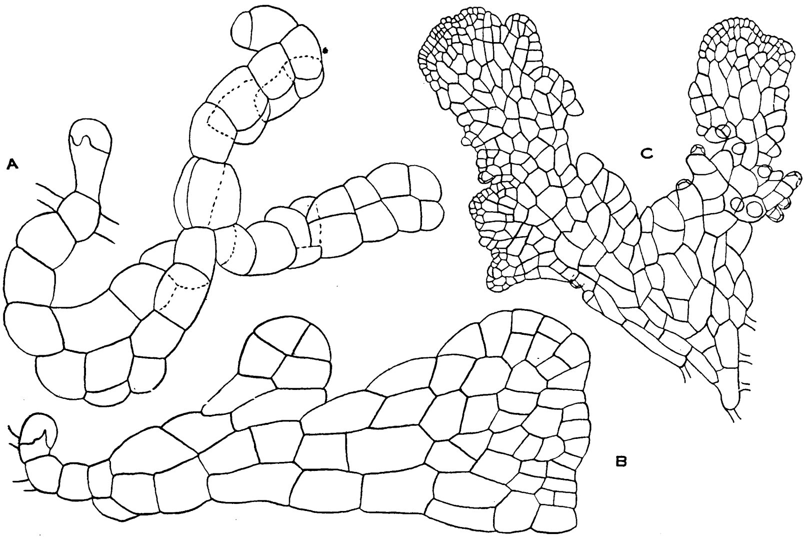

FIG. 10. A, B. Branched prothallia of *Asplenium bulbiferum* Forst., × 75. C. Branched prothallium of *Asplenium platyneuron* (L.) Oakes, × 75.

Asplenium platyneuron (L.) Oakes.—FIG. 10, C, shows a prothallium of this species which developed in a crowded region on a soil culture. In this case branching occurred at a later period in the development of the prothallia. No filament was formed in the early development of the prothallium, but the second cell by division gave rise immediately to the beginnings of an expanded cell plate which during development branched dichotomously. Each branch in turn formed a distinct growing region at its apex.

Asplenium bulbiferum Forst.—The two examples of branched prothallia which are shown in FIG. 10, A, B, developed on the distilled water culture. In both cases the branches originated after the expanded portion of the prothallia had been formed. In FIG. 10, A, the branching was dichotomous. This example is especially interesting as showing the tendency of the prothallium to revert to a filamentous condition at the time of the formation of the filamentous branch. In FIG. 10, B, branching was monopodial and the branch tended to form immediately a plate of cells.

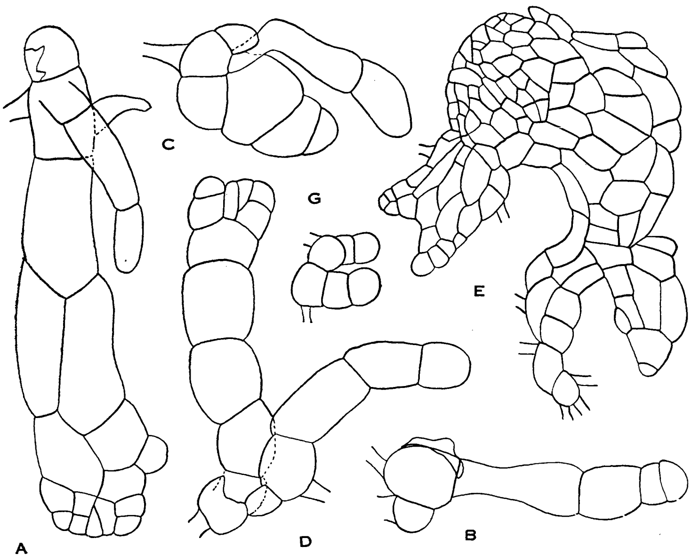

FIG. 11. A–E. Branched prothallia of *Phegopteris polypodioides* Fée, × 125. G. Branched prothallium of *Polypodium aureum* L., × 125.

Phegopteris polypodioides Fée.—The branched prothallium which is shown in FIG. 11, A, occurred in an uncrowded region of the soil culture while those shown in FIGS. 11, B–E, and 12, F, developed in modified Prantl's solutions. FIG. 11, B–D, was found in the Prantl's solution with K_2SO_4 omitted, while FIGS. 11, E, and 12, E, occurred in Prantl's solution from which $CaSO_4$ had been omitted. In all cases observed the branching was monopodial. In FIG. 11, A, the branch was filamentous in form and originated in the second cell of the filament. FIG. 11, B, shows the origin of the branch from the first cell of the filament and FIG. 11, D, shows the further development of this branch into a filament of five cells. In FIG. 11, C, is shown an interesting example of branching. Here the first prothallial cell instead of dividing by a transverse wall into two cells, divided by means of a longitudinal wall, thus forming two cells side by side. One of these cells by growth and transverse division continued the growth of the filament while the other gave rise to two branches. One formed a filament of two cells, the first of which was extremely long. In FIGS. 11, E, and 12, the branches were not formed until the expanded portion of the prothallia had begun to develop. In FIG. 12, the expanded portion later showed a decided tendency to branch monopodially at its apex.

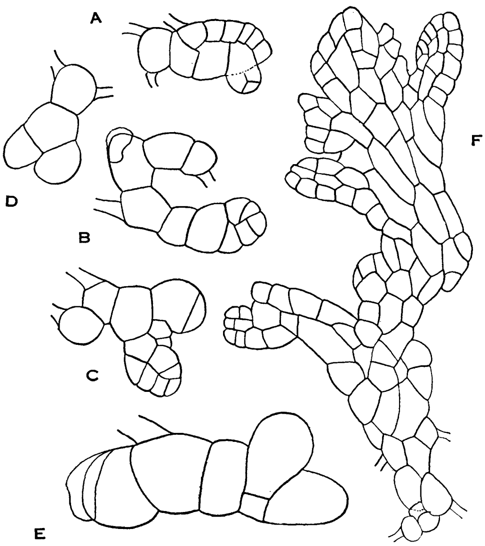

FIG. 12. A–E. Branched prothallia of *Woodsia obtusa* (Spreng.) Torr., × 125. F. Branched prothallium of *Phegopteris polypodioides* Fée, × 75.

Polypodium aureum L.—Only one case of branching was observed in this species and it developed on the distilled water culture. As shown in FIG. 11, G, the branch originated in the first prothallial cell. The rate of growth was the same for both the main filament and the branch.

Woodsia obtusa (Spreng.) Torr.—All the cases of branched prothallia of *Woodsia obtusa* were observed on distilled water cultures; in two cases branching was dichotomous while in the other three cases it was monopodial. FIG. 12, B, shows the branch originated from the first cell of the filament. In FIG. 12, A, the branch originated from the slightly developed cell plate. FIG. 12, C, D, shows different stages in the development of the dichotomous branches. FIG. 12, E, was an interesting case of branching. Here the wall which cuts off the branch from the main filament did not form at the usual place, but formed almost in the center of the filament cell which gave rise to the branch.

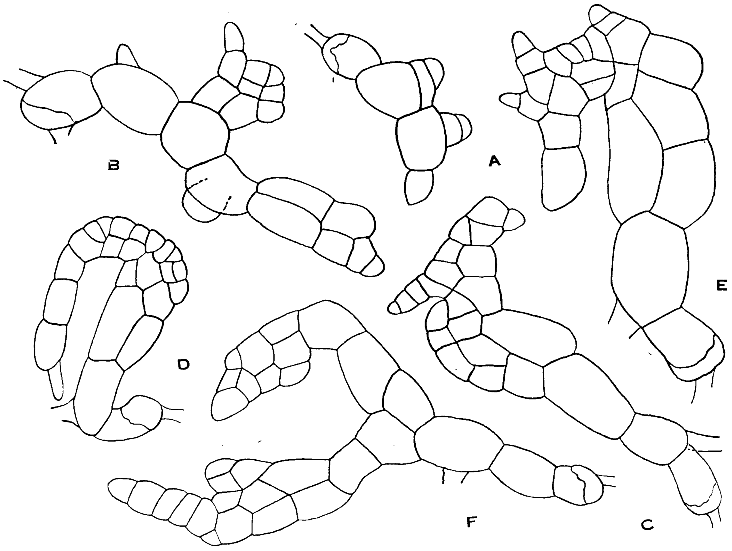

FIG. 13. Branched prothallia of *Scolopendrium vulgare* Sm., × 125.

Scolopendrium vulgare Sm.—All cases of branching in this genus were observed on Prantl's solution with $CaSO_4$ omitted. FIG. 13, A–E, shows typical examples of the types of branching found in these cultures. FIG. 13, A, is interesting as showing the tendency of both the second and third cells of the filament to form monopodial branches with very short cells. In FIG. 13, B, the branch which originated from the third cell of the filament formed immediately a plate of cells which in turn showed a tendency to branch at one side of the apex. Fig. 13, C, shows the origin of a branch from the apex of the expanded portion of the prothallium, while Fig. 13, D, E, shows further development of such a branch. These branches formed a small plate of cells, two rows in width, then tended to revert to a filamentous condition, at the same time growing downward, thus giving the appearance of two young prothallia attached by their apexes. Fig. 13, F, shows the only case of dichotomous branching which was observed. One of the branches reverted from a plate of cells to a filament four cells in length.

Woodwardia virginica (L.) Sm.—The branched prothallia of

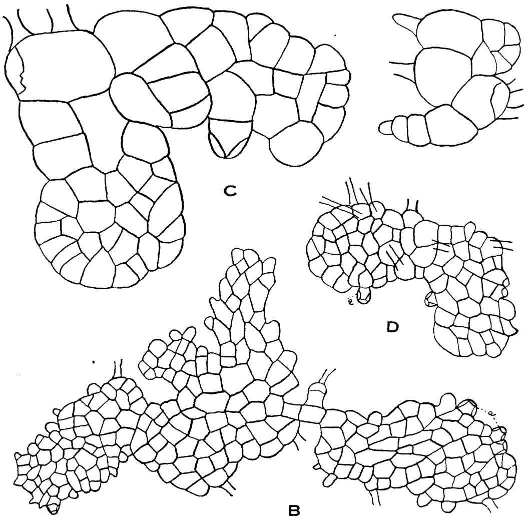

Fig. 14. Branched prothallia of *Woodwardia virginica* (L.) Sm. A, D, × 125; B, C, × 75.

Woodwardia virginica varied in size and shape and showed a decided tendency to branch dichotomously. Those shown in Fig. 14, A–D, and 15, E, F, developed on the inner surface of the pot wall of the soil culture. They were not crowded by other prothallia and were well lighted. Fig. 15, G, developed on Prantl's nutrient solution with $CaSO_4$ omitted. In Fig. 14, A, B, branching took place from the first and second cells of the filament. In Fig. 14, C, D, and 15, G, branching took place after the plate of cells had begun to develop, while in FIG. 15, E, F, branching occurred much later in the development of the prothallia.

Pteridium aquilinum (L.) Kuhn.—The only example of branching observed in this species was on Prantl's full solution (FIG. 15, H). Here the branch developed from the second cell of the filament and seemed to show a more vigorous growth than the main filament. The branch formed a short filament of two cells, then developed the beginnings of an expanded region while the main filament developed three cells of irregular length before cutting off the beginnings of an apical cell. This slowness in growth and the irregularity of length of the cells of the filament would seem to indicate a poorly nourished condition of the main filament.

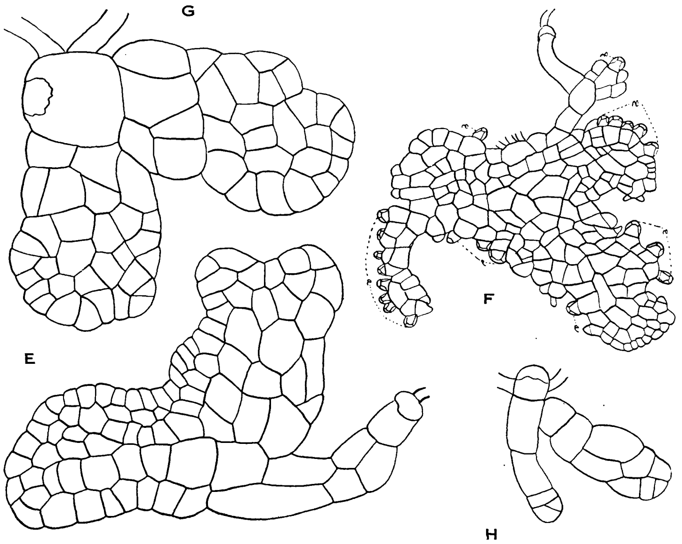

FIG. 15. E–G. Branched prothallia of *Woodwardia virginica* (L.) Sm., × 75; *a*, antheridia. H. Branched prothallium of *Pteridium aquilinum* (L.) Kuhn, × 125.

DISCUSSION

A comparison of the previously described branched prothallia with those found by other writers would seem to indicate that whatever factor, or set of factors, working separately or together, may have been the determining ones, the development of branches was associated with conditions of the environment. In Klebs's experiment weak light seemed to have been the cause of branching. Light may be the determining factor in branching where the prothallia are crowded and therefore shaded by other prothallia, but it can not be considered the determining factor in all the cases described in this paper, for the majority of these branched prothallia occurred in uncrowded regions of the cultures under good light conditions. However, all the branched prothallia except one developed on cultures of distilled water or nutrient solutions, from which some chemical element had been omitted; while all but two of the branched prothallia on the soil cultures were found on the inner surface of the pot wall. This is especially interesting as indicating that other factors than light entered into the problem. Atkinson designates the branched prothallia of *Adiantum* as "starved prothallia," which would seem to indicate that they had developed under poor nutritive conditions. Miss Black suggested the possibility of a lack of oxygen as the determining factor in the production of the branched prothallia in her cultures. This explanation would not hold good for the present cases, as all three cultures, distilled water, soil, and nutrient solution, were covered with loosely fitting glass plates and, since the prothallia were not submerged in the nutrient solution or distilled water they received a sufficient supply of oxygen.

As branching was not observed in the nutrient solution cultures, where all the chemical elements necessary for growth were present in sufficient quantities to meet the needs of the prothallia; as few cases of branching were observed among the prothallia of the soil cultures, in positions which appeared favorable for nutrition, it would seem as if there was an intimate connection between nutrition and branching, that poor nutritive conditions accelerated the stimulus of branching, and that good nutritive conditions weakened the stimulus. However, it is impossible to say just what factor of nutrition was the determining one; for even by cultivating prothallia on nutrient solutions whose chemical formula are known, we do not know the physiological effect from the chemical reactions due to the presence or absence of various chemical elements.

SUMMARY

1. Branched prothallia occurred in cultures of *Adiantum bellum*, *A. Capillus-Veneris*, *A. cardiochlaena*, *A. cuneatum*, *A. trapeziforme*, *Asplenium bulbiferum*, *A. Filix-femina*, *A. platyneuron*, *Camptosorus rhizophyllis*, *Onoclea sensibilis*, *Phegopteris polypodioides*, *Pteridium aquilinum*, *Scolopendrium vulgare*, *Woodsia obtusa*, and *Woodwardia virginica*.

2. Branched prothallia were not confined to one type of culture medium, but developed on distilled water, on soil and on nutrient solutions.

3. Branches were not developed at any definite period in the life history of the prothallia, but were formed: (*a*) by any cell of the filament; (*b*) by divisions of the last cell of the filament; (*c*) from the margin and apex of the expanded portion of the prothallium.

4. Branching was both dichotomous and monopodial.

5. A definite relation seemed to exist between branching and nutrition.

In conclusion I wish to express my thanks to Professor Alexander W. Evans of Yale University and to Dr. C. H. Kauffman of the University of Michigan, to both of whom I am indebted for valuable suggestions in the preparation of this paper.

YALE UNIVERSITY

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